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The Role - Activity and/or Processing - Of (Re) Active Oxygen Species in Desiccation Sensitivity and/or Tolerance, Development, Dormancy and/or Germination in Seeds

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Abstract

The contents of cells may comprise and/or consist of up to 80% water. Removal of cellular water may be accompanied by and/or associated with disruptions and/or disturbances of normal cellular events and/or organization. Desiccation tolerance has evolved adaptations - mechanisms and/or processes - to deal with the situation. Dehydration, germination and ageing may lead to the generation and/or production of free radicals. (Re)active oxygen species may result in cellular damage and/or death. Antioxidants detoxify and/or process free radicals. Active oxygen species may also be involved and/or participate in an integrated intracellular signaling network. This paper attempts an overview and/or review of free radical processes – activity and/or processing - in seed desiccation sensitivity and/or tolerance in the context and/or light of the latter.

Keywords: (Re)active oxygen species; Ageing; Antioxidants; Cell Signaling; Detoxifying (and/or processing) enzymes; Free radical(s and/or activity); Germination; Oxidative stress

Introduction

The free-radical theory of ageing originated in the medical sciences more than half-a-century ago [1]. It was later introduced into seed science when Kaloyereas [2] argued that lipid oxidation might underlie loss of viability in seeds.

The role of free radical activity in seed deterioration in germinating orthodox and recalcitrant seeds as a result of drying has been supported by evidence from studies over a period of two decades [3-10]. Berjak and Pammenter [11] suggested that the recent interest may be a result of implication of (re)active oxygen species (ROS and/or AOS) in an intracellular signaling network. This review happens in the backdrop and/or background of the implication of AOS and/or ROS in intracellular signaling.

Nature and origin – generation and/or production - of (re)active oxygen species

Oxygen is a slightly reactive molecule that may give rise to the strongly reactive and/or potentially harmful (re)active oxygen species during electron transport processes of cellular photosynthesis and/or respiration [12]. Reduction of oxygen leads to the formation of the superoxide radical ($O^{2-\cdot}$).

The superoxide radical is a molecule with an uncoupled electron and/or can react with other molecules to stabilize its energy. However, superoxide itself is not highly reactive and is short-lived but can further form hydrogen peroxide (H_2O_2) and the hydroxyl radical (OH.).

Hydrogen peroxide may result from the non-enzymatic reduction of O^{2-} in the presence of H^+ ions and/or from the action of catalase on $O^{2-\cdot}$. H_2O_2 has a strong oxidizing capacity and its life span - half-life of 1 ms - is longer than that of superoxide - half-life of 2 μs. H_2O_2 can also diffuse through membranes and/or therefore reach target molecules at some distance from its production site.

The Haber–Weiss and Fenton reactions involve superoxide radicals and H_2O_2 and/or lead to the formation of the Hydroxyl Radical ($OH^{\cdot}$). $OH^{\cdot}$ is the most aggressive form of the oxygenated derivatives in the presence of iron and/or other transition metals.

AOS include the radical derivatives of oxygen ($O2^{-\cdot}$, OH, and/or peroxyl, alkoxyl and/or hydroperoxyl radicals) and/or non-radical derivatives of oxygen such as H_2O_2, ozone and/or singlet oxygen (O_2^*) [13]. Free radicals are molecular species containing one or more unpaired electrons. Many AOS sources have been identified in plants [12]. Any transfer and/or transport chain of electrons towards oxygen can potentially generate ROS.

Orthodox seeds are devoid of an important source of AOS through photosynthetic electron transport in chloroplasts except in the early developmental phase. The photosynthetic electron transport chain leads to the production of superoxide and singlet oxygen.

Moreover, the seed water content and metabolic activity change dramatically from the beginning of development to the end of germination. Therefore, the sources of AOS in seeds also probably vary considerably.

The mitochondrial respiratory chain is one of the major sources of AOS; electron leakage from the transport chain generates superoxide and subsequently H_2O_2 by dismutation of the former [14].

Approximately 2 to 3% of the oxygen used by the mitochondria can be converted into superoxide and H_2O_2 in normoxic conditions [15,16]. The amount of H_2O_2 produced is thus directly proportional to respiratory activity [17].

Respiration is intense during the first stages of embryogenesis in orthodox seeds but strongly decreases during the desiccation phase on the mother plant and shuts down when seeds are quiescent [18]. It is estimated that mitochondrial respiration ceases at water contents lower than 0.25 gg^{-1} dm [19]. Germination, on the other hand, is associated with a strong increase in the respiratory activity and enhanced production of AOS.

Peroxisomes are also a possible source of AOS. Several types of these organelles are frequently distinguished: glyoxysomes present in oily seeds, leaf-type peroxisomes of photosynthetic tissues, nodule-specific peroxisomes from uninfected cells of Leguminosae nodules and/or gerontosomes found in senescing tissues [20,21].

Glyoxysomes play a key role in mobilization of lipid reserves of oily seeds. They contain the enzymes of β-oxidation and the glyoxylate cycle which convert lipid reserves into sugars during the first stages of seedling development [22].

Fatty acid β-oxidation produces H_2O_2 resulting from the activity of enzymes such as glycolate oxidase. In addition, the oxidation of xanthine into uric acid by xanthine oxidase in the peroxisomal matrix is associated with the production of superoxide and seems to be common to all the types of peroxisomes [23,24]. The potential role of these organelles in free radical biology and/or oxidative stress is generating increased research interest.

Indeed, peroxisomes are also the site of localization of catalase which eliminates H_2O_2 and/or of the production of Nitric Oxide (NO), a compound now considered to play a major role in cellular signalling in plants [24,25].

Other sources of AOS have been characterized more recently in plants including NADPH oxidases of the plasma membrane which transfer electrons from cytoplasmic NADPH to oxygen. These enzymes give rise to the superoxide radical that subsequently dismutates to H_2O_2.

NADPH oxidases are involved in the 'oxidative burst' during plant–pathogen interactions [26,27], in various plant growth and development processes [28] and/or plant responses to various forms of abiotic stress [29]. NADPH oxidase is involved in abscisic acid (ABA)-induced generation of AOS during water stress for example [30,31].

pH dependent cell-wall peroxidases and amine oxidases may also lead to the formation of H_2O_2 in the apoplast particularly during biotic stress [32-34]. While it is likely that mitochondria and peroxisomes are the major sources of AOS in non-quiescent orthodox seeds, further work is required to evaluate the contributions of these and/or other sites of ROS production to seed development and germination. It is also necessary to distinguish the production sites from the action sites because they are often distant from one another. For example, recent work has shown that transmembrane aquaporins and peroxiporins may play a role in the transport of H_2O_2 in vegetative tissue [29,35] but the mobility of AOS in seeds has not, as yet, been documented.

Finally, non-enzymatic autoxidation of lipids may also represent a potential source of AOS in seeds particularly during dry storage when enzymatic activities and metabolism are negligible. Lipid autoxidation would generate free radicals that would be trapped in seed tissues [36-38].

In conclusion, orthodox seeds are devoid of an important source of AOS through photosynthetic electron transport in chloroplasts except in the early developmental phase, the sources of AOS in seeds also probably vary considerably, the mitochondrial respiratory chain is one of the major sources of AOS, peroxisomes are also a possible source of AOS, other sources of AOS have been characterized more recently in plants including NADPH oxidases of the plasma membrane and/or pH-dependent cell-wall peroxidases and/or amine oxidases and/or non-enzymatic autoxidation of lipids may also represent a potential source of AOS in seeds particularly during dry storage when enzymatic activities and metabolism are negligible. More research is clearly needed to establish all the sources of AOS and their relative contributions during the different stages in seeds.

Dual nature - signaling and/or toxicity - of (re)active oxygen species

The uncontrolled accumulation of AOS, particularly of $OH^{\cdot}$, which cannot be eliminated enzymatically, is highly toxic. ROS can react with the majority of biomolecules resulting in oxidative stress that can become irreversible and/or cause cellular damage.

Many harmful effects of AOS on cellular macromolecules have been identified. Among these, one of the best known is lipid peroxidation because it has been studied intensively in food science in order to prevent rancidity of fatty products.

Lipid peroxidation is a free-radical chain process leading to the deterioration of polyunsaturated (free) fatty acids (PU[F]FAs). It is initiated by free-radical attack upon a lipid resulting in the removal of a hydrogen atom from a methylene group adjacent to a double bond.

In aerobic conditions, the carbon radical, originating from the abstraction of hydrogen, is stabilized by oxygen and yields a peroxyl radical ($ROO^{\cdot}$) which is capable of removing a hydrogen atom from another fatty acid chain to form a Lipid Hydroperoxide (LOOH) in a propagation step [13]. Lipid peroxidation is likely to degrade PU(F)FAs present in membranes and/or in reserve lipids of oily seeds. Nucleic acids and proteins are also potential targets of AOS.

The hydroxyl radical can directly damage both nuclear and organelle DNA because it attacks deoxyribose, purines and pyrimidines [39] whereas neither superoxide nor H_2O_2 seem to have such a deleterious effect.

Enzymes can be inactivated easily by AOS when amino acids essential for, or close to, the active sites are degraded. Again, the hydroxyl radical seems to be the most reactive species regarding protein sensitivity to oxidative stress since it can damage a great range of amino acids.

Hydrogen peroxide is also known to react with thiol groups and can directly lead to inactivation of some enzymes such as those of the Calvin cycle [40]. Beside these effects on enzymes, AOS can also damage transport proteins, receptors and ion channels and then lead to extensive cellular dysfunction [13].

Whereas AOS toxicity is well established, cellular antioxidant mechanisms seem to tightly control ROS concentrations rather than to eliminate them completely suggesting that some AOS might play normal physiological roles and/or act as signaling molecules.

Following the numerous studies carried out in animal cellular biology, the possible roles of AOS as messengers of various signal transduction pathways are being evaluated in plants. It was established that H_2O_2 acts as a second messenger in mammalian cells in the early 1970s [41].

The role of this molecule was investigated later in plants. Chien and Lin [42] were among the first to show that H_2O_2 is involved in the tolerance to various abiotic stresses. Levine et al. [43] also showed that H_2O_2 may elicit cellular defense reactions against pathogens.

Since then, many processes involving H_2O_2 have been identified in plants including Programmed Cell Death (PCD) [44-48], somatic embryogenesis [49], response to wounding [50], root gravitropism [51] and/or ABA-mediated stomatal closure [52,53]. The roles of superoxide and/or other AOS in signaling pathways are less well described so far; however, O2-· seems to play a part in cell death and plant defense [54,55].

At the cellular level, events regulated by H_2O_2 are beginning to be identified. They include protein phosphorylation through Mitogen-Activated Protein Kinase (MAP kinase) cascades [56-58], calcium mobilization [59,60] and/or regulation of gene expression [61,62].

In summary, many harmful effects of AOS on cellular macromolecules have been identified including one of the best known in lipid peroxidation, nucleic acids and proteins are also potential targets of AOS and/or enzymes can be inactivated easily by AOS. However, the possible roles of AOS as messengers of various signal transduction pathways are being evaluated in plants.

Control of (re)active oxygen species levels: antioxidants

With regard to the possible roles of AOS previously considered, it appears necessary for the cells to be equipped with mechanisms allowing elimination (in the case of oxidative stresses) and/or homeostasis of ROS (for cellular signaling). Various enzymatic and nonenzymatic mechanisms play these roles in plants.

Superoxide dismutase can be mitochondrial - MnSOD, cytosolic - Cu/ZnSOD and/or chloroplastic – CuZnSOD and/or FeSOD. SOD dismutates superoxide radicals into H_2O_2 and oxygen [63].

Hydrogen peroxide is eliminated by the action of catalase (CAT). CAT is located in glyoxysomes and peroxisomes except the isoform Cat-3 of maize which is mitochondrial [64].

The ascorbate–glutathione cycle, also called the Halliwell–Asada cycle, may also take part in H_2O_2 scavenging; it involves Ascorbate Peroxidase (APO/X), Monodehydroascorbate Reductase (MDAR), Dehydroascorbate Reductase (DHAR) and Glutathione Reductase (GR). The enzymes of this cycle are present in chloroplasts, the cytoplasm, mitochondria, peroxisomes and/or the apoplast and/or participate in the regeneration of the powerful antioxidants ascorbic acid (vitamin C [AsA]), reduced glutathione (GSH) and α-tocopherol (vitamin E [α-toc]).

The role of the ascorbic system in seeds has been reviewed by De Tullio and Arrigoni [65]. Glutathione peroxidases (GPX) may also catalyse the reduction of H_2O_2 and/or hydroperoxides [66]. Various compounds such as polyphenols, flavanoids and/or peroxiredoxins [67] also have a strong antioxidant function.

In conclusion, various enzymatic and nonenzymatic mechanisms allow elimination and/or homeostasis of ROS. Again their location and relative contributions require further investigation.

(Re)active oxygen species during seed development: acquisition of desiccation tolerance

Embryogenesis, reserve accumulation and/or maturation (and/or) drying are the three typical stages of orthodox seed development on the mother plant leading from a zygotic embryo to a mature and/or quiescent seed. Most research contributions dealing with AOS and seed development have, up to now, concerned the final stage of seed desiccation in relation to acquisition of dehydration tolerance, a common feature of all orthodox seeds. However, some studies have also shown that ROS metabolism might also be important during initial embryogenesis and seed filling.

Metabolic activity and mitochondrial respiration are high during embryo development. Moreover, some developing embryos contain functional chloroplasts with photosynthetic activity but the contribution of the latter to seed filling seems to vary greatly among species [18].

This observation suggests that developing embryos have the potential to generate significant amounts of AOS necessitating tight control by antioxidant mechanisms. The ascorbate system seems to play a central role in embryogenesis and cell growth [65] mainly because ascorbate may control cell-cycle progression [68].

Recently, it has also been proposed that ascorbate content could influence cell growth by modulating the expression of genes involved in hormonal signaling pathways [69]. Studies carried out in the fields of in vitro micropropagation and somatic embryogenesis may yield complementary insights on the roles of AOS in embryo development.

During zygotic and somatic embryogenesis, activities and/or expression of the main antioxidant enzymes, CAT and SOD, vary greatly. In Arabidopsis, MnSOD expression increases during early embryo development [70]. SOD and CAT activities also increase during development of horse chestnut somatic embryos [71] and/or during development of oak microcuttings [72].

Totipotency of plant protoplasts has also been related to the activity of the cell antioxidant machinery since a direct correlation exists between high AOS content and repressed expression of totipotency [73].

Conversely, AOS may also play a positive role in growth and development. The differentiation of embryogenic cells of *Lycium barbarum* is promoted by a transient decrease in CAT activity resulting in high cellular H_2O_2 for example [49].

It has also been postulated that hydroxyl radicals are involved in cell-wall extension during cell growth by causing oxidative scission of polysaccharides [74-78]. This aspect has been mainly studied in seedling growth and/or will be discussed further regarding the roles of AOS in seed germination.

The possible involvement of AOS in seed-filling processes is less well documented. Hydrogen peroxide is suspected to participate in lignin deposition in the cell walls in a peroxidase-catalysed reaction. In developing barley grains, the involvement of a diamine oxidase in H_2O_2 production has been demonstrated along with lignin deposition in the chalazal cells [79].

Apoplast lignification and/or its subsequent separation from the symplast ensures that assimilates move into the endosperm via the symplast only [80] which suggests that H_2O_2 might play a role in the control of grain filling. The regulation of CAT gene expression has

been studied intensively throughout the development of maize kernels by Scandalios et al. [64].

These authors have shown that a temporal and spatial distribution of CAT isoforms occurs. Among the three genes, Cat1, Cat2 and Cat3, which code for the three CAT isoforms in maize, Cat3 is expressed during early post-pollination kernel development whereas Cat1 and Cat2 are expressed later [64]. The same authors have suggested that differential catalase gene expression during embryo development might be regulated by the phytohormones ABA and auxin [81,82]. De Gara et al. [83] have followed the changes in detoxifying enzyme activities during maturation of *Triticum durum* kernels. Their results show that seed filling is associated with a high potential of the H_2O_2 detoxification machinery mainly due to CAT and APO/X activities.

As mentioned previously, studies dealing with the involvement of AOS in seed development have focused mainly on the acquisition of desiccation tolerance. The ability of developing orthodox seeds to withstand severe desiccation generally appears during the phase of reserve accumulation approximately midway through development but it depends on the drying rate which affects seed survival after drying [84-86].

AOS generation is known to occur during dehydration of various plant tissues [87] and/or in recalcitrant seeds [5]; it might result from metabolic imbalances leading to leakage of high-energy intermediates from plastids and/or mitochondria [16,19,88,89].

Therefore, desiccation tolerance might be related, at least in part, to the cellular ability to scavenge these compounds to avoid deleterious AOS-related damage [5,19,90]. Desiccation damage and/or tolerance of developing orthodox seeds are largely suspected to be related to oxidative processes.

The possible role of antioxidant systems in desiccation tolerance has been studied more during drying of recalcitrant seeds [85] and/or during dehydration of germinated seeds [3,91] than during seed development in planta probably because the latter studies are not easy to implement. Nevertheless, acquisition of desiccation tolerance in bean seeds seems clearly to be associated with a reorientation of the enzymatic antioxidant defense systems.

Dried and/or mature orthodox seeds display high CAT and GR activities and low SOD and APO/X activities whereas the reverse is the case in immature recacitrant seeds [92]. The decrease in APO/X activity during seed desiccation seems to be common to seeds of other species such as *Vicia faba* [93] and *Triticum durum* [83] as already mentioned by De Tullio and Arrigoni [65] suggesting that the ascorbate system is probably not involved in desiccation tolerance.

Interestingly, it has also been demonstrated that desiccation of developing sunflower seeds is associated with an increase in CAT activity thus leading to decreased H_2O_2 content and lipid peroxidation damage [94,95]. This study has made it possible to identify the catalase gene as being finely regulated at the transcriptional level by the loss of water which is in accordance with the data obtained with cotton [96] and maize [64] seeds.

Although several other ROS-scavenging enzyme genes such as those coding for SOD and GR are upregulated by dehydration in plants [97,98], data about their regulation during seed desiccation are less clear than for CAT and APO/X and/or do not permit a construction of a clear picture of their possible roles in this process. For example, GR activity increases at the onset of dehydration tolerance in French bean seeds [92] whereas it does not change significantly during desiccation of sunflower seeds [94] and decreases in the case of wheat seeds [83].

Accumulation of non-enzymatic antioxidant components might also play a role in protecting cells against AOS during desiccation. Indeed, it must be emphasized that the in vivo enzyme activities are closely related to the cell water content.

At low moisture contents, water is tightly bound on to macromolecular structures thus decreasing molecular mobility and accessibility of enzymes to their substrates. As enzymatic activities are usually measured in vitro in aqueous media, they may not necessarily reflect their behavior in situ.

This situation suggests that prevention of oxidative damage at low water contents might be more likely related to AOS scavenging by antioxidant compounds. The (reduced) Glutathione/Oxidized Glutathione (GSH/GSSG) ratio is suspected to be involved in withstanding drying but it has been little investigated during acquisition of desiccation tolerance of orthodox seeds. Nevertheless, high GSSG contents have been observed in dry seeds of pea [99] and tomato [100].

Peroxiredoxins (Prxs) are thiol-dependent antioxidants capable of reducing H_2O_2 and $OH^{\cdot}$. They accumulate in seeds during maturation drying [67]. 1Cys-peroxiredoxin seems to be expressed only in those barley seed tissues that survive during desiccation [101]. Finnie et al. [102] have also shown that the protein 1Cysperoxiredoxin occurs at the onset of drying in barley ears. Furthermore, Prxs would play a particular role in protecting nuclear integrity thus preserving genetic information during desiccation [101].

LEA (late embryogenesis abundant) proteins are the proteins most often cited as accumulating during drying. Their presence generally correlates with desiccation tolerance but their biological functions remain unclear [103]. Interestingly, it has been demonstrated that dehydrins, a group-2 LEA class of proteins, could act as free-radical scavengers [104]. If this role was ubiquitous, it may strengthen the importance of AOS scavenging in dehydration tolerance mechanisms.

Complementary data on putative roles of AOS in desiccation damage and/or tolerance are available from studies on recalcitrant seeds, resurrection plants and germinated seeds. They generally provide information similar to those observed with orthodox seeds.

Acquisition and loss of desiccation tolerance are closely related to the capacity of cells to scavenge AOS. Loss of viability during drying of recalcitrant seeds of *Quercus robur* [105], *Shorea robusta* [6] and *Theobroma cocoa* [7] is accompanied by a loss of the cellular antioxidant potential and/or an accumulation of free radicals.

Desiccation and rehydration of the resurrection plant *Xerophyta viscose* [98] and/or germinated maize [90] and/or wheat seeds [91] are also associated with changes in the balance of AOS content and/or detoxifying enzyme activities.

Taken together, these data suggest a critical role of antioxidants in preventing dehydration-related damage and allowing acquisition of desiccation tolerance. They also imply that the ability of cells to withstand loss of water might be closely related to AOS scavenging. However, other protective mechanisms must not be ruled out and the cell antioxidant machinery must be considered as a part of a wider arsenal of weapons against desiccation stress.

When dealing with involvement of AOS in seed development, one often considers only their potentially toxic effects. Nevertheless, they

may have a beneficial role in embryo growth. They are increasingly considered as playing a key part in cell signaling.

The variations in AOS contents observed during seed maturation could, therefore, be involved in the shift of gene function from a developmental to a germinative mode which is supposed to be initiated by seed dehydration [84]. Indeed, AOS are known to regulate the expression of many genes.

In Arabidopsis, H_2O_2 induces 113 genes and represses 62 others for example [62]. However, the mechanisms allowing control of gene expression by AOS in plants are still largely unknown. One of the most cited possibilities concerns the activation of transcription factors by redox status changes [106,107].

Alternatively, gene promoter regions may possess antioxidant response elements (ARE motifs) suspected to play a role in either H_2O_2 and/or antioxidant sensing as is the case for the maize catalase Cat1 gene [64].

Finally, seed development is generally required to allow the embryo to produce a viable and/or vigorous seed capable of germinating in a wide range of environmental conditions and/or permitting species survival. Changes in antioxidant compounds and/or enzymes during seed development should also be regarded as a prerequisite for obtaining a vigorous seed. It will be seen below that a vigorous seed has to be endowed with a full antioxidant machinery to avoid oxidative stresses that occur during germination.

In summary, ROS metabolism needs to be studied during all stages of development not only maturation (and/or) drying, the ascorbate system may play a central role in embryogenesis and cell growth mainly because ascorbate may control cell-cycle progression and/or totipotency of plant protoplasts has also been related to the activity of the cell antioxidant machinery since a direct correlation exists between high AOS content and repressed expression of totipotency. Conversely, AOS may also play a positive role in growth and development such as hydroxyl radicals involvement in cell-wall extension during cell growth by causing oxidative scission of polysaccharides and/or possible hydrogen peroxide participation in lignin deposition in the cell walls in a peroxidase-catalyzed reaction.

In conclusion, the possible effect and/or influence on differential antioxidant enzyme gene expression during embryo development by the phytohormones ABA and auxin, the possible association of the acquisition of desiccation tolerance with a reorientation of the enzymatic antioxidant defense systems, the possible accumulation of the various non-enzymatic antioxidant components in protecting cells against AOS during desiccation particularly at low water concentrations, the possible role of the various LEA proteins as free-radical scavengers and/or the possible beneficial role of ROS in cell signaling and/or regulation of gege expression require further investigation.

AOS and seed dormancy and/or ageing: (loss of) desiccation tolerance

The inability of seeds to germinate in apparently favorable environmental conditions is referred to as dormancy [18]. Dormancy can either result from an inhibitory action of the covering structures or reside within the embryo itself.

In some cases, seed-coat-imposed dormancy can be alleviated with oxidants such as H_2O_2 which can oxidize the phenolic compounds present in the seed envelopes. This action allows improved oxygenation of the embryo during seed imbibition [108,109].

It can also cause cracking in the coat of hard seeds thus facilitating their imbibitions [42]. More interesting are the roles that endogenous AOS and antioxidants might play in regulating seed dormancy but these roles are poorly documented up to now.

Nevertheless, several lines of evidence suggest that H_2O_2 alleviates seed dormancy: it stimulates the germination of dormant seeds of barley [108,110,111], rice [112], apple [113] and/or *Zinnia elegans* [109].

Morohashi [114] also showed that chemicals that inhibit in vitro catalase activity promoted the germination of dormant seeds of lettuce and pigweed. However, the cellular basis of these effects remains unclear.

It has been postulated that H_2O_2 causes an activation of the oxidative pentose phosphate pathway owing to the oxidation of reduced NADPH [108]. One attractive alternative hypothesis regarding the involvement of H_2O_2 in seed dormancy release concerns its effect on ABA content.

Wang, et al. [110,111] have demonstrated that treatment of dormant barley seeds with H_2O_2 results in a decrease in endogenous ABA level. Bogatek, et al. [113] have shown that alleviation of apple embryo dormancy by cyanide induces a decrease in ABA content occurring concomitantly with an increase in H_2O_2. The control of seed dormancy by ABA might, therefore, be connected with H_2O_2 signaling. This interplay has to be explored fully in future studies.

In summary, the role of AOS in dormancy breakage directly and/or indirectly via signaling needs further study.

(Re)active oxygen species and seed germination: loss of desiccation tolerance

Germination sensu stricto is associated with many cellular, metabolic and/or molecular events rendering the radicle able to emerge from the seed. Only this phase of the germination process shall be considered here which precedes visible signs of radical extension keeping in mind that other AOS generating mechanisms such as fatty acid oxidation may occur during early seedling growth.

The reactivation of metabolism following seed imbibitions may provide an important source of AOS. H_2O_2 is produced at the early imbibitions period of soybean [16,88,115], radish [28], maize [116], sunflower [117], wheat [118] and/or tomato [115] seeds for example.

Accumulation of other AOS such as NO [119], hydroxyl radicals [28] and/or superoxide radicals [28,88,115] also occurs during germination of seeds of various species. Nevertheless, the exact sites of AOS generation during germination are not known precisely; embryonic axes, seed coats and/or aleurone layers have been proposed as such putative sites of synthesis.

The production of AOS by germinating seeds has often been regarded as a cause of stress that might affect the success of germination. Therefore, antioxidant compounds and enzymes have been widely considered as being of particular importance for the completion of germination.

The antioxidant compounds α-tocopherol [120-122], flavonoids and/or phenolics [120,122,123] increase during germination.

Ascorbate and reduced glutathione, two related antioxidants, also increase during early seed imbibition [65,99,122,124,125].

The two latter compounds might play a wider role than the sole scavenging of AOS through control of the cellular redox balance [125] and/or protein synthesis [126]. Protection against oxidative stress during imbibition has also been suggested for peroxiredoxins [67]. 1-Cys Prxs are synthesized during rehydration of the desiccation-tolerant moss *Tortula ruralis* [127] and/or in germination of buckwheat seeds [128].

The other battery of AOS detoxifying and/or scavenging enzymes also displays important changes during seed imbibition and germination. CAT and GR activities increase prior to radicle protrusion, the latter being concomitant with the elimination of H_2O_2 and/or the limitation of lipid peroxidation in germinating sunflower seeds [117,129].

Similar stimulation of CAT activity and/or expression during germination has also been reported in seeds of maize [64,82,116], soybean [88,115] and/or Arabidopsis [130]. Interestingly, a quite tight relationship between CAT activity and germination rate exists in sunflower seeds [131].

The enhancement of seed germination by priming has also been associated with stimulation of CAT activity in sunflower [129,131], soybean [132] and/or sweet corn [133] and/or of CAT expression in Arabidopsis [130]. Tanida [134] has demonstrated that germination rate at a suboptimal temperature is positively correlated with CAT activity in rice grains.

Conversely, slow germination of aged seeds seems to be associated with low CAT activity in sunflower [117,135], soybean [136] and maize [137]. Changes in other detoxifying enzymes during seed imbibition and germination are less well-documented than for CAT although there is a general trend for stimulation of the activities of these enzymes. This trend is the case for SOD [88,115], APX [65] and/or GR [125].

Comparative analysis of changes in antioxidant enzymes and/or compounds and in AOS during germination therefore brings together several lines of evidence supporting a role for AOS scavenging in seed germination. Radicle protrusion occurs at the time when AOS content reaches a steady-state level as illustrated in many cases.

In this regard, AOS production resulting from tissue rehydration appears to be a negative event that has to be counteracted. Even though this aspect is plausible and is quite well documented in the literature, AOS production during germination should also be regarded from a different point of view.

In light of the increasing progress made in the understanding of cellular mechanisms driven by AOS, the role of AOS in seed germination perhaps needs to be revisited. To date, at least four putative distinct roles for AOS, apart from their toxic effects, have been identified.

As mentioned previously, AOS and particularly H_2O_2 may induce expression of many genes including those coding for defence-related proteins, transcription factors, phosphatases, kinases and/or enzymes involved in AOS synthesis or degradation [29,62]. Additionally, AOS may also regulate genes through changes in cellular redox status [107].

AOS might also intervene in the cell-wall modification required for elongation of the radicle, the first sign of the completion of germination. Hydroxyl radicals, produced from O_2- and H_2O_2 by cell-wall peroxidases in vivo [138], can lead to cell-wall loosening processes underlying cell expansion [75,76].

Hydroxyl radicals may break down polysaccharides by an oxidative scission of backbone bonds [75,76], a process that could be involved in radicle protrusion. Radicle protrusion requires weakening of the micropylar region of the endosperm in tomato seeds, for example [139]. Several hydrolases - mannanase, cellulase, glucanase - have been suspected to contribute to cell-wall loosening [139].

However, a peroxidase activity develops in the tomato endosperm cap prior to radicle emergence [114]. This activity, which generates OH·, might be involved in the cell wall loosening processes, allowing cell expansion to occur. Recently, Schopfer et al. [77] have also suggested that auxin might promote cell growth through O2-production and the subsequent generation of hydroxyl radicals.

It has also been supposed that production of AOS and their release in the surrounding medium during seed imbibition play a part in protecting the embryo against pathogens [28]. Many studies indicate that ROS produced during the early phase of pathogen attacks trigger pathogen-resistance responses, acquired systemic resistance and/or programmed cell death [26,27]. The possible involvement of AOS in protection of the growing embryo against a hazardous environment constitutes a seductive hypothesis that needs to be addressed properly.

Finally, AOS are also suspected to be involved in Programmed Cell Death (PCD) in the aleurone layer of cereal grains. PCD occurs during germination after the aleurone cells have synthesized and/or secreted hydrolytic enzymes into the endosperm for mobilizing stored reserves and/or is under the control of gibberellins and/or ABA [87,140,141]. PCD would result from a down-regulation of the antioxidant enzymes in barley aleurone layers thus leading to overproduction of ROS and membrane rupture [46].

In conclusion, the reactivation of metabolism following seed imbibitions may provide an important source of AOS. Nevertheless, the exact sites of AOS generation during germination are not known precisely; embryonic axes, seed coats and/or aleurone layers have been proposed as such putative sites of synthesis. In addition in light of the increasing progress made in the understanding of cellular mechanisms driven by AOS, the role of AOS in seed germination perhaps needs to be revisited.

Conclusion

AOS and antioxidants probably play a wider role in seed physiology than is currently appreciated as illustrated by the studies reviewed elsewhere and/or here. AOS may be involved in all the stages of seed life from development to germination but the general picture of their action is certainly very complex because they must be considered as part of a signaling network involving numerous regulatory components.

Many questions related to the roles of AOS in seed physiology have to be addressed. Progress is required in determining their cellular production sites and/or their diffusion within the cell taking into account the unique aspects of seed tissue physiology in particular the dramatic changes in moisture content and metabolic activity that occur in the life of the seed.

Elucidating the mechanisms underlying the interplay of AOS with hormones is also a challenge for future research in this area. Such investigations will without any doubt encourage revisiting the cellular

mechanisms involved in acquisition of the desiccation tolerance, germination and alleviation of dormancy.

Analyses of gene expression in contrasting situations using the novel methods developed in recent years such as microarrays, cDNA amplification fragment length polymorphism (cDNA-AFLP) and proteomic tools will be of help in answering some of these questions.

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